carina, rather sparsely punctate, sides pieces more coarsely and densely punctate; abdomen moderately punctate. Length 9 mm.

Southwestern Texas (Chapman Grant).

A narrower and smaller insect than our other species of *Plastocerus* from all of which it differs in the carinate prosternum. The antennal rami are shorter, less densely ciliate and with shorter hairs than in *schaumii* or *megalops* and are nearly as in *frater*.

THE ORDERS AND RELATIONSHIPS OF APTERYGOTAN INSECTS.[1]

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The ancestors of the Arthropoda were, in all probability, very similar to Annelidan worms, and, although the Annelida, like all recent forms, have developed many characters peculiar to themselves, certain members of the group have preserved some exceedingly primitive features, which enable us to infer what the ancestors of Arthropods must have been like.

Although the discussion of the probable lines of descent leading up to the development of the Insectan type of Arthropod is beyond the province of the present paper, it may be remarked that the "Apodidæ" have departed but little from the condition which was doubtless characteristic of the ancestral Crustacea, and such Crustaceans as *Apus* and *Branchippus* (which are not far removed from such Trilobites as *Triarthrus, Neolenus* and *Nathorstia*) have departed but little from the probable ancestral condition of Arthropods in general. These Crustacea and Trilobita, then, present as nearly as any Arthropods now known, the characters present in the earlier forms, and enable us to gain some idea of what the common ancestors of the Arachnida, Merostoma, Trilobita, Crustacea, "Myriapoda" (*sensu lato*), Hexapoda, etc., were like.

[1] Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

In the development of recent Arthropoda, the lines of descent which have the most closely paralleled the line of descent of the Insecta, are those of the Crustacea, Diplopoda, Chilopoda and Symphyla (see fig. 2). Indeed, the Crustacea, "Myriopoda" (*i. e.,* Chilopoda, Diplopoda, and Symphyla) and Insecta, may be regarded as forming the three apices of a triangle, each of whose apices is connected with the other two by mutual bonds of relationship. Among the Crustacea, the Arthrostraca (*e. g., Anaspides, Koonunga, Bathynella,* etc.) and have retained certain characters suggestive of the ancestral condition of insects, but, on the whole, the "Myriopoda" (*sensu lato*) and *Scolopendrella* in particular, are more closely related to the Insecta than any other Arthropods.

The parts of the head, legs, and abdominal appendages of the Apterygotan insects are strikingly like the corresponding parts of the "Myriopoda," and even with regard to their embryological details, the Apterygota are very like "Myriopods," as has been pointed out by Philiptschenko, 1912, Lignau, 1911, Heymons, and others. Furthermore, the points wherein the Apterygota differ most from higher insects, are those wherein they approach more closely to the "Myriopoda" and Crustacea, and from the standpoint of comparative anatomy and embryology, there can be no doubt that the Apterygotan insects are the most primitive—and have therefore departed the least from the probable ancestral condition of insects in general.

Despite the fact that the paleontological record is confessedly incomplete, and notwithstanding the fact that such extremely fragile and rare insects (for they have apparently never been very numerous) could not be expected to leave many traces in the lower strata, which have been subjected to great pressure and upheaval, Handlirsch and his followers would use the lack of Apterygotan remains in the earlier strata as an argument against the view that the Apterygota should be regarded as the nearest living representatives of the ancestors of the Pterygotan forms. In their efforts to widen the gap between the Apterygota and Pteryigota, these authors would even go so far as to remove the Apterygota from the class Insecta (or Hexapoda) and would place them in a distinct class, or classes by themselves! The fact remains, however, that from a morphological point of view (and aside from the presence or absence of wings) there is an infinitely wider gap between the Blattidæ and Chalcididæ—

which Handlirsch and his followers unhesitatingly group in the same class—than there is between the Blattidæ and Lepismatidæ—which they would not group in the same class. In the same way, an immature Plecopteron such as a nymph of *Peltoperla*, is structually far closer to *Lepisma* than it is to *Pulex*, or any of the higher Pterygotan insects—and in the last analysis, comparative anatomy (whether it be the comparative anatomy of embryos, or of living or fossil adults) furnishes us with the only reliable material for determining relationships!

Since the Apterygotan forms, such as *Lepisma*, etc., are so closely related to the lowest Pterygota (such as the Blattidæ, nymphs of *Peltoperla*, etc.) and since the various Apterygotan groups are intimately bound together by intermediate forms—as is also the case with the Pterygotan groups—the attempt to place the Apterygota in a class, or classes, not included in the class Insecta, is wholly unwarranted, and fails to take into consideration the fundamental structural similarities which underlie all groupings based upon relationship! The Apterygota are as much "Insecta" as the Pterygota are, and if the Apterygota are to be split up into several "classes," then the Pterygota also must be split up into several "classes" in order to be consistent. This, however, is neither necessary nor desirable, since the grouping of the class Insecta into two sub-classes, the Apterygota (or Apterygogenea) and Pterygota (or Pterygogenea) is based upon structural similarities, and expresses the actual relationships with sufficient accuracy.

Prell's division of the Insecta into two subclasses, the *Anamerentoma* (Protura) which exhibit a postembryonic increase in the number of abdominal segments, and the *Holomerentoma* (all other insects), which exhibit no postembryonic increase in the number of abdominal segments, fails to take into consideration the close anatomical relationship of the Protura to such forms as *Tomocerus*, etc., which exhibit no such postembryonic increase in the number of abdominal segments; and while Prell's subdivision is very useful from the standpoint of the study of the different types of "metamorphosis," the old subdivisions Apterygota and Pterygota (proposed by Brauer, and modified by Lang) are more useful from the standpoint of the study of relationships. In this connection, it may be further remarked, that in such Dipterous larvæ as *Scenopinus, Thereva, Bibio,*

Ceroplatus, etc., there is a sort of increase in the number of the abdominal segments, by the interpolation of "intercalary" segments, formed by the lengthening and demarcation of the intersegmental region—although this is not strictly comparable to the type of true segmental increase exhibited by the Protura.

Although the Apterygota form a well-defined group, quite distinct from the Pterygota, I do not know of any key which will enable one who has no preconceived idea of the true nature of an insect (especially with regard to the larval and wingless forms) to place it correctly in every case. I would therefore offer the following key as a purely tentative effort to supply this lack.

1. Mouthparts either retracted in cavity of head, or practically wanting, or not mandibulate 2
   Mouthparts not retracted in cavity of head, but mandibulate 3
2. Ventral region of the abdomen bearing either styli, vestigeal legs or ventral tube .....*Apterygota.*
   Abdomen without styli, vestigeal legs, or ventral tube .....*Pterygota.*
3. Abdomen with more than one pair of styli .....*Apterygota.*
   Abdomen with at most one pair of styli, usually none .....*Pterygota.*

The styli referred to in the preceding key, are paired, movable, spine-like appendages, borne at the posterior margin of certain of the abdominal sternites, and are not homologous wtih the entire vestigeal legs, but are appendages of the basal segment of the legs, and occur on the meso- and metathoracic coxae in such insects as *Machilis,* and on the basal segment of the leg in certain "Myriopoda." The vestigeal legs mentioned in the key are true leg-vestiges—whether they are homologous with the so-called false legs (pseudopodia) of larval Lepidoptera, etc., has been questioned. The ventral tube (which represents the united vestigial legs of the first abdominal segment) is an adhesive organ situated in the mid-ventral line of the first abdominal segment, and may be large and columnar, or it may be reduced to the merest vestige, requiring close scrutiny to detect it.

The Apterygota may be divided into two supersections, the *Eustyligera,* or styli-bearing Apterygota, and the *Astyligera,* or non-styli-bearing Apterygota, according to the presence or absence of styli in the two groups.

The styli-bearing Apterygota (Eustyligera) are also cerci-bearing in all cases thus far observed, the non-cerci-bearing form "*Aniso-*

sphæra" described by Tomosvary as related to the Lepismatidæ, having subsequently been proved to be a larva of the beetle *Cephennium.* The antennæ are usually well developed and consist of more than six segments. No postantennal organ has been observed in members of this group.

The second super-section, or non-styli-bearing group (Astyligera) usually lacks segmented cerci and forceps-like terminal abdominal structures, in addition to the styli. The "cerci" of *Tomocerus* and others of the group (to which Willem, Folsom, and others have called attention) are not segmented, and there is some question as to whether they are to be considered as strictly homologous with the true cerci of the other forms, although this point has not been sufficiently investigated to be definitely decided. The antennæ may be lacking in this group, but if present, are usually composed of not more than six segments—although an "annulation," or "ringing" of the terminal segments, sometimes occurs. The postantennal organ, or its homologue, is frequently present; but may be wanting.

All of the members of the non-styli-bearing group have mouthparts of the concealed type (*i. e.,* entognathous or cryptognathous) the mouthparts being retracted into the cavity of the head, as in *Eosentomon, Tomocerus, Entomobrya,* etc. On the other hand, some of the styli-bearing group have mouthparts of the concealed type (the mouthparts being retracted into the cavity of the head, as in *Campodea, Japyx,* etc.) while others of the group have mouthparts of the exposed type (ectognathous or gymnognathous) as in *Lepisma, Machilis,* etc.

There are apparently three main lines of evolution represented in the Apterygota. In other words, the Apterygotan insects group themselves about three principal centers. These are represented by the Protura (*e. g., Eosentomon,* etc.) the Rhabdura (*e. g., Campodea,* etc.) and the Thysanura (*Lepisma,* etc.) and the insects forming these groups may be regarded as representing the three principal sections of the sub-class Apterygota.

The lowest or most primitive section of the Apterygota comprises those insects which group themselves about the Protura (such as *Eosentomon, Acerentomon,* etc.) which have departed as little as any from the probable ancestral condition of the group as a whole. These insects form the section *Proturadelphia* or "Proturan-brother-

hood" and are characterized as follows. Styli absent, and segmented cerci wanting, although unsegmented appendages termed "cerci" may be present in such forms as *Tomocerus,* etc. Mouthparts of the concealed type in all of the members of the group. Uropods, or true abdominal legs usually present, either in the form of the vestigeal abdominal legs of the Protura, or the modified abdominal legs which form the ventral tube (columella), tenaculum, and springing apparatus (or furcula) of the other members of the section. Antennæ may be absent as in the Protura, although Schepotieff, 1909, has figured and described them for "*Protapteron*"—but this is stated to be a "*lapsus calami,*" by Prell, and others. In other forms the antennæ are usually short and composed of only six segments—although an "annulation" of the terminal antennal segments occurs in certain members of the group. The so-called "pseudoculus" of the Protura, and the postantennal organ of the other forms, are doubtless the homologues of Tömösvary's organ in the "Myriopoda." In addition to this, the general character of the alimentary tract, the reproductive organs, the segmentation of the egg, and the embryological development, etc., of the members of this group, clearly suggest "Myriopodan" affinities. Some of the families contained in this section (which is the only non-styli-bearing one) are the Eosentomidæ, Acerentomidæ, Neelidæ, Sminthuridæ, Achorutidæ, Entomobryidæ, etc.

The second section (which is a division of the styli-bearing Apterygota) comprises those insects which group themselves about the Rhabdura (*Campodea,* etc.) forming the section *Rhabduradelphia,* or "Rhabduran-brotherhood." In some respects, such forms as *Anajapyx* are more primitive than the true Rhabdura (such as *Campodea*), but the term Rhabdura, being better known, has, on this account, been chosen to illustrate the group as a whole. In the insects belonging to this section, styli are usually borne on the first seven abdominal sterna, but may be lacking on the first (*Campodea*). Cerci, in the form of paired segmented caudal filaments, or modified to form the forceps-like terminal abdominal appendages of *Japyx,* etc., occur in all of the members of the group thus far observed; but a median unpaired terminal caudal filament (characteristic of the next group to be considered) is always wanting. All of the members of this section have mouthparts partially or wholly of the con-

cealed type (entognathous or cryptognathous), but a postantennal organ is usually wanting. Eyes are absent in most of the members of the group. The antennæ are usually well developed and are usually composed of many segments. Segmented uropods may occur on the basal abdominal segment (as in *Campodea*) although they are usually greatly reduced or lacking. Eversible sacs, etc., are found on certain of the abdominal sterna in some members of the group. There is usually a "Y"-shaped suture in the meso- and metasternum (of the thorax), and a longitudinal cranial suture, together with a transverse occipital suture, usually occurs in the insects of this section. The tarsi are usually apparently one-segmented, and the abdomen is composed of ten or eleven segments. Maxillary palpi apparently one- or two-segmented. Abdominal ganglia seven or eight in number. The principal families of this section are the Campodeidæ, Projapygidæ and Japygidæ. The insects composing this group might in some ways be regarded as occupying a position somewhat intermediate between the insects of the first section (Protura-delphia) and the one next to be considered.

The third section (which is also a division of the styli-bearing Apterygota) comprises those insects which group themselves about the Thysanura (*Lepisma,* etc.) forming the section *Thysanuradelphia,* or "Thysanuran-brotherhood." Such forms as *Machilis,* or *Præmachilis,* are more primitive, or have departed less from the ancestral condition of the group, than the true Thysanura (such as *Lepisma*) have, but the designation Thysanura, being the best known of the terms applied to the members of the group, has been chosen to typify the section as a whole. Styli are found at least on the terminal abdominal segments of practically all members of the group, and in certain forms, such as *Machilis, Præmachilis,* etc., styli are borne on the coxæ of the meso- and metathorax as well. Unlike the insects of the preceding section, the members of this group usually possess a median unpaired caudal filament, in addition to the paired caudal filaments or cerci, although the cerci may be absent in rare instances (*Dasyleptus*). All of the insects belonging to this section have mouthparts of the exposed type (ectognathous or gymnognathous). Segmented uropods are usually absent, and postantennal organs are wanting in the members of the group. The eyes are usually well developed, although absent in some cases, and the

antennæ are usually well developed and are composed of many segments in most insects belonging to this section. When the caudal filaments are short, the antennæ are usually correspondingly reduced. Protrusile sacs occur on certain of the abdominal sterna in some cases. Tarsi two or three-segmented, and abdomen with traces of eleven segments. Maxillary palpi four or five-segmented. Abdominal ganglia eight in number. Some of the families belonging to this section are the Machilidæ, Lepismatidæ, Gastrotheidæ, etc.

The relationships of these three lines of descent to the higher insects, and to the other Arthropods are rather puzzling. It may be remarked, however, that the Proturon type exhibits indications of affinities with such Plecoptera as *Capnia, Leuctra,* etc., on the one hand, and with such Crustacea as *Bathynella* and other Anomostraca on the other. The Rhabduron type offers suggestions of affinities with the Plecoptera (and the closely related Dermaptera) and with the Symphyla such as *Scolopendrella.* The Thysanuran type exhibits indications of a relationship with such Plecoptera as nymphs of *Peltroperla* on the one hand, and with certain Crustacea, such as *Ligia,* on the other. Since the Crustacea, "Myriopoda" and Insecta are so closely related, however, it is merely to be expected some of the Apterygota would retain characters suggestive of a relationship to the Crustacea while others show a marked relationship to the "Myriopoda," since all are connected by mutual bonds of relationship, and members of the Apterygota would naturally retain characters suggestive of both Crustacea and "Myriopods."

The Rhabduran section is, on the whole, more closely related to the Thysanuran section than to the Proturan section, but all three lines are rather sharply demarked and apparently represent three distinct lines of development, just as there are similar distinct lines of development in the Pterygotan insects. These three sections, too, exhibit differences of a greater value than that of distinct orders. Indeed, there is a far greater difference between *Machilis* and *Campodea,* than there is between *Perla* and *Phasma,* and the difference between *Machilis* and *Lepisma* (or *Nicoletia*) is as great, or greater, than that between *Merope* and *Sialis.* Furthermore, if the latter examples represent distinct orders, then *Machilis* and *Lepisma* should be placed in distinct orders, to be consistent. The value which one will attribute to these differences depends upon the individual him-

self, and as long as human nature remains as it is, we will have some who are "lumpers," and some who are "splitters." Of recent entomologists, however, those who are so "ultra-conservative" as to be unwilling to admit of more than one Apterygotan order, the "Aptera," are in a decided minority, and one is led to suspect that they have either not made a detailed study of the insects in question, or an overweening desire for "unity and simplicity" has caused them to cling to a system of classification but little removed from the ancient Linnean one!

As time goes on, and as the structural details of the Apterygotan insects have been more carefully worked out, it becomes more and more evident that the general superficial resemblances between many of the insects classed together in the older groupings, are far outweighed by the differences in their morphological details. I would therefore fully agree with Handlirsch and his followers (such as Brues and Melander, Escherich, etc.) in their contention that the heterogeneous collections of insects comprising the old "orders" should be re-grouped into several distinct orders whose members are more closely related.

In the following key, the greater part of the insects referred to belong to distinct orders although I would not maintain that this is true of all of them, as will be discussed later. In accordance with the quite widely accepted custom, I have designated the Apterygotan orders by terms ending in "-ura" (*e. g.,* Protura, Rhabdura, Thysanura, etc.), rather than by Handlirsch's terms ending in "-oidea," since the latter termination is preëmpted by groups of superfamily rank (*e. g.,* Muscoidea, Ichneumonoidea, etc.). Handlirsch's method of using a well-known family name to typify the group as a whole, however, has much to recommend it, since it is self-explanatory, I have therefore made use of a modification of this method in the following key, merely for the sake of convenience, using the termination "oides" (rather than the preëmpted termination "oidea") in connection with the name of a well-known family, thereby immediately calling to mind the representatives of the group as a whole.

1. Styli and segmented caudal filaments or terminal forceps present.....2
   Styli and segmented caudal filaments or terminal forceps wanting.....7
2. Mouthparts not retracted into cavity of head 3
   Mouthparts retracted or concealed in cavity of head.....5

3. With but one (the median) terminal caudal filament.
Dasyleptoides (Mononemura).

With three caudal filaments 4

4. Head in frontal view deeper than broad. Styliform appendage usually found on coxa of meso- and metathorax. Tarsi usually three-segmented.
Machioides (Trinemura).

Head in frontal view broader than deep. No styliform appendage on coxa of meso- and metathorax. Tarsi usually two-segmented.
Lepismatoides (Thysanura).

5. Styli present on first abdominal sternum. Abdomen with terminal forceps, or with segmented cerci 6

Styli wanting on first abdominal sternum. Abdomen with segmented cerci, whose terminal segment is imperforate .... **Campodeoides (Rhabdura).**

6. Abdomen with segmented cerci whose terminal segment is provided with an apical aperture .....**Projapygoides (Prodicellura).**

Abdomen with forceps .....**Japygoides (Dicellura).**

7. Vestigeal legs of first abdominal segment united and modified to form a ventral tube (in some cases reduced to a mere vestige). Antennæ usually present. Abdominal segments usually not exceeding six in number....8

Vestigeal legs of first abdominal segment not united to form a ventral tube. Antennæ usually absent. Abdominal segments usually nine to twelve in number .....**Eosentomoides (Protura).**

8. Abdomen sub-cylindrical: segments usually distinct.
Entomobryoides (Euarthrura).

Abdomen sub-globular: segments wholly or in part grown together.
Smithuroides (Synarthrura).

There is some doubt as to whether the fossil Dasyleptidæ constitute a distinct order, or are merely to be regarded as a suborder of the forms with three caudal filaments. The Projapygidæ also might better be regarded as a suborder of the Dicellura (Japygidæ), than as a distinct order. Brues and Melander group them with the Rhabdura (Campodeidæ) in an order in which the Japyigidæ are not included; but if the Projapygidæ are not to be considered as forming a distinct order, they should be grouped with the Dicellura (Japygidæ), since their affinities are with the Dicellura, rather than with the Rhabdura (Campodeidæ). Handlirsch and his followers regard the Entomobryidæ and Sminthuridæ as representing distinct orders, while Boerner (who gave them the names Arthropleona and Symphypleona) regards them as representing suborders rather than as distinct orders.

It is possible that such insects as *Troglopedetes* (family Troglo-

pedetidæ), described by Joseph, may constitute an order or suborder; but, aside from the fact that they are strongly aberrant, blind forms, with four-segmented maxillary palpi, the known details of their anatomy are too meager to determine this point.

The relationships of the different groups are brought out in the following descriptions, in which are discussed the more important characters of the different groups, which could not be treated in detail in the preceding key.

Non-Styli-Bearing Apterygota (Astyligera).

I. *Section Proturadelphia.*

This section might be divided into two subsections, on the basis of the presence or absence of the ventral tube (or its homologue), but a further division is apparently unnecessary.

1. Eosentomoides (Protura).—Styli absent. Cerci, or forceps-like terminal abdominal appendages, ventral tube, and springing apparatus wanting. Mouthparts retracted in cavity of head. Labial palpi present. Mandibles and labium somewhat similar to those of *Tomocerus,* as is true of the ventral groove of the head region. Postantennal organ (the "pseudoculus") usually present. Eyes wanting. The antennæ described and figured for "*Protapteron*" (*Eosentomon*) by Schopotieff probably belong to some other insect, so that all members of the group thus far studied lack antennæ, the forelegs being modified to serve as tactile organs in the place of the lost antennæ. Abdominal segments of the adult insect usually twelve in number, although at first only nine—a postembryonic increase in the number of abdominal segments being peculiar to these insects. The basal two or three abdominal segments usually bear vestigeal legs. Abdominal ganglia usually six in number (*Acerentulus*). The principal families contained in the group are the Acerentomidæ and Eosentomidæ.

2. Entomobryoides (Euarthrura).—Styli absent. Segmented cerci, or forceps-like terminal abdominal appendages wanting. The uropods (or abdominal legs) of the first abdominal segment are more or less grown together and modified to form the ventral tube (columella) whose vesicles are usually short and sac-like. The

uropods of the third abdominal segment form the tenaculum, when present, and those of the fourth or fifth abdominal segment form the springing apparatus (furcula) when present. Mouthparts retracted in cavity of head. Labial palpi wanting. Postantennal organ usually present. Eyes present or absent. Antennæ usually four- to six-segmented. Head rounded and directed straight forward (prognathous) or obliquely downward. Body comparatively long, and the abdomen sub-cylindrical. Abdominal segments, which do not exceed six in number, usually free or distinct (whence the name Euarthrura). There is no postembryonic increase in the number of abdominal segments. Abdominal ganglia wanting, or united with the last thoracic ganglion. Heart with six pairs of ostia. The principal families of the group are the Achorutidæ and Entomobryidæ.

If the preceding group be regarded as of the value of an order, it might be divided into two suborders as follows: (*a*) The "Eupodura," including those forms in which the springing apparatus is usually well developed, and is generally attached to the penultimate segment (although in some Isotomas it is attached to the antepenultimate segment). The head is directed obliquely downward, and scales usually occur on members of this subdivision. Examples are *Isotoma, Orchesella,* etc. (*b*) The "*Pauropodura,*" including those forms in which the springing apparatus is reduced or wanting, and when present is attached to the antepenultimate instead of to the penultimate segment. The head is directed straight forward, the body is usually granular, and scales are absent. Examples are *Podura, Achorutes, Anurida, Neanura,* etc.

3. SMINTHUROIDES (SYNARTHRURA).—Styli absent. Segmented cerci, or forceps-like terminal abdominal appendages wanting. Uropods of first abdominal segment more or less grown together and modified to form the ventral tube, whose vesicles may be long and tubular, or short and sac-like. Springing apparatus usually present. Mouthparts retracted in cavity of head. Labial palpi wanting. Postantennal organ usually absent. Antennæ, with few exceptions, elbowed and four-segmented. Head rounded and usually vertical in position (*i. e.,* directed downward). Body short and abdomen subglobular. Thoracic and abdominal segments more or less closely united (whence the name "Synarthrura"). No postembryonic increase in the number of abdominal segments. Abdominal ganglia

wanting (or united with the last thoracic ganglion). Heart extending backward only about one third the length of the abdomen, and with only two pairs of ostia. Tracheal system usually wanting, but when present is best developed in *Sminthurus* and *Sminthurides*. There is no anastamosing between tracheæ of opposite sides of body as in higher insects. The principal families of the group are the Neelidæ and Sminthuridæ.

Of the three groups mentioned above, the *Protura* are by far the most primitive, and have preserved many characters which were doubtless present in the ancestral insects. The *Euarthrura* (or Entomobryid group) are rather closely related to the Protura, but represent a somewhat degenerate and specialized offshoot which branched off from the Proturan line at a comparatively early period of development, and has become specialized in a different direction. The *Synarthrura* (or Sminthurid group) are very closely related to the Entomobryid group; but on the whole are more highly specialized than the latter.

Styli-Bearing Apterygota (Eustyligera).

II. *Section Rhabduradelphia.*

4. Campodeoides (Rhabdura).—Styli and paired segmented cerci present, but median caudal filament wanting. Mouthparts retracted into cavity of head. Apex of mandible dentate, with a dentate plate attached below it. Maxillary palpi one-segmented. Antennæ slender, many jointed. Eyes and postantennal organ usually wanting. Transverse occipital suture distinct, and occipital region comparatively large. Body not scaled. Abdomen composed of eleven distinct segments (the eleventh being very small and reduced). First abdominal segment with a pair of uropods, or vestigeal abdominal legs, but no styli occur on the first segment. Styli and protrusile sacs usually occur on abdominal segments two to seven, inclusive. The long slender segmented cerci have no opening at the tip of the terminal segment for the discharge of glands (as in the Projapygidæ). Anal laminæ distinct. Abdominal ganglia seven in number. Spiracles confined to the thoracic region (three in number). Malpighian tubes represented by papillæ. Ovaries simple, without ovarioles. Heart with nine pairs of ostia. This order contains the family Campodeidæ.

5. PROJAPYGOIDES (PRODICELLURA).—Styli and segmented cerci present, but median unpaired caudal filament wanting. Mouthparts retracted, and mandibles similar to those of the preceding group. Maxillary palpi two-segmented (?). Antennæ rather robust, or less slender than in preceding group. Eyes and postantennal organ usually wanting. Transverse occipital suture not distinct, and occipital region reduced. Body not scaled. Body composed of eleven distinct segments, the eleventh being reduced and covered by the tergum of the tenth. First abdominal segment with a pair of somewhat cylindrical or conical processes, one on each side of the midventral line: the first abdominal segment is also provided with a pair of styli (absent in the preceding group) which are somewhat long and cylindrical. Styli occur on abdominal segments one to seven inclusive. Two rather short, robust cerci composed of fewer segments (about six in all) than in the preceding group, occur in these insects, and the terminal segment of each cercus bears an opening at the tip for the discharge of glands. Anal laminæ distinct in adults. Seven abdominal ganglia. Seven pairs of spiracles in abdominal region. Malpighian tubules represented by five or six small short tubes or papillæ. Ovarioles present. Heart with nine pairs of ostia. Foregut extends posteriorly to the fifth abdominal segment. This group contains the family Projapygiidæ. Its position is intermediate between the Campodeidæ and Japygidæ, the type of mandibles, the segmented cerci, the presence of vestigeal malpighian tubules, etc., being Campodeidan characters; but the general character of the body (and its appendages, other than the cerci) is much more like that of the Japygidæ than the Campodeidæ, and if the group is to be regarded as a suborder rather than as an order, it should be placed with the Japygidæ in the order Dicellura, instead of with the Campodeidæ in the order Rhabdura—as Brues and Melander have done!

6. JAPYGOIDES (DICELLURA).—Styli present, but the cerci have become modified to form a pair of unsegmented terminal forceps-like structures. Median terminal caudal filament wanting. Mouthparts retracted. Mandibles with dentate apex, but the dentate plate found in the Projapygidæ and Campodeidæ is absent. Maxillary palpi two-segmented. Antennæ rather robust or less slender than in Campodeidæ. Eyes and postantennal organ usually absent. Occipital suture not distinct, and occipital region reduced. Body not

scaled. Abdomen apparently composed of ten segments, the tenth and eleventh being more or less closely united. First abdominal segment with two submedian hairy papillæ, and also bearing a pair of short stout spine-like styli (unlike the rather long slender styli of the Projapygidæ) which likewise occur on segments two to seven inclusive. The cerci are represented by imperforate forceps-like terminal appendages. Anal laminæ not distinct in adults. Eight abdominal ganglia. Seven pairs of spiracles in abdominal region. Malpighian tubules wanting. Seven ovarioles present. Foregut extending posteriorly only to metathorax (not to fifth abdominal segment as in Projapygidæ). This order contains the family Japygidæ (to which may be added the Projapygidæ, if the latter are not to be regarded as representing a distinct group).

The Campodeidæ are more primitive than the Japygidæ, although they are apparently not much (if any) more primitive than the Projapygidæ. The Projapygidæ, as was mentioned above, occupy a position intermediate between the Japygidæ and Campodeidæ. They are regarded by some investigators as the lowest of living insects but the Protura are more primitive in many respects (although they have become strongly modified in certain structural details). The Campodeidæ and Projapygidæ may possibly be regarded as occupying a position somewhat intermediate between the Protura and the next group to be considered.

III. *Section Thysanuradelphia.*

7. Dasyleptoides (Mononemura).—This group comprises the family Dasyleptidæ founded on the fossil insect *Dasyleptus lucasi,* described by Brongniart as follows. Body cylindrical, tapering posteriorly, and terminated by a single multiarticulate filament, which is as long as the body. Antennæ and legs robust. Head quite large. Prothorax very short, and meso- and metathorax, which are of equal size, much longer than the prothorax. Abdominal segments ten in number, and equal in size; the last, which bears a multi-articulate filament, a little longer than the others. Some specimens appear to have abdominal plates similar to those found in *Machilis.* The entire body (antennæ, legs, thorax and abdomen) covered with numerous very short hairs. The body, including the terminal abdominal

filament, varies from fifteen to twenty-two millimeters in length. This insect resembles *Lepisma* and *Machilis* morphologically, but differs from them in many respects chief among which is the occurrence of but a single caudal filament. This group contains the family Dasyleptidæ. Although here ranked as an order, the group (which is related to the Machilidæ) may possibly be of the value of suborder only; but this point can be determined only upon a more detailed study than has been given the subject by Brongniart.

8. MACHILOIDES (TRINEMURA).—Three caudal filaments (a median unpaired terminal filament, and a pair of lateral filaments homologous with the cerci) occur in this group. Head usually directed downward (hypognathous), not flattened dorso-ventrally, but laterally compressed, in frontal view deeper than broad. Eyes usually large, and extending forward above the antennæ are approximate or almost contiguous above. They are composed of relatively numerous small ommatidia. Mouthparts of the exposed type: maxillary palpi usually seven-segmented. Pronotum usually shorter than mesonotum. Thoracic sterna not in the form of broad plates overlapping the coxæ somewhat laterally (as in the next group to be considered). Coxæ subcylindrical: those of the meso- and metathorax usually provided with styliform appendages. Tarsi usually three-segmented. Abdomen composed of eleven segments, the tergum of the tenth not partially covering the eleventh. Body subcylindrical, tapering posteriorly, and is usually clothed with scales. Insects usually capable of springing. Abdominal ganglia eight in number. Seven pairs of spiracles in the abdominal region. The tracheæ of one side of the body do not anastomose with those of the other side nor are those of the same side connected by longitudinal trunks, the tracheæ being arranged segmentally. There are twelve malpighian tubules. Ovaries wtih seven ovarioles. Heart with nine pairs of ostia. This group contains the family Machilidæ.

9. LEPISMATOIDES (THYSANURA).—Two segmented cerci, in addition to the median unpaired terminal caudal filament, occur in this group. The unpaired median filament according to Heymons, is merely a prolongation of the body which has become annulated, and is therefore not strictly comparable to the paired filaments, which are homologous with cerci. In this group, the head is usually directed forward (prognathous) and is flattened dorso-ventrally, in frontal

view broader than deep. Eyes, when present, always small and situated on the side of the head, never extending above the antennæ or approximate above. They are composed of relatively few, large, separate ommatidia. Mouthparts of the exposed type. Maxillary palpi usually five-segmented (six-segmented in *Thermophila*). Pronotum usually longer than, or as long as the mesonotum. The thoracic sterna usually in the form of broad plates projecting somewhat over the coxæ laterally. Coxæ usually broad and flattened; those of the meso- and metathorax devoid of styliform appendages. Tarsi usually two-segmented. Abdomen composed of eleven segments, the tergum of the tenth usually partially covering the eleventh. Body usually depressed, or flattened dorso-ventrally, thus differing from the more cylindrical Machilidae, although Ridley describes a specimen of *"Lepisma" corticula* of which he states that "the chief peculiarity of this *Lepisma* is its very rounded back, resembling that of a *Machilis* rather than that of a typical *Lepisma*." The body is usually scaled, although in such forms as *Nicoletia* and the Maindroniidæ, the scales are absent. Brues and Melander are thus not strictly correct in stating that in the members of this group "the body is always clothed with scales." The number of abdominal ganglia is eight, and there are eight pairs of spiracles in the abdominal region. The tracheæ anastamose ventrally with those of the opposite side of the body, and those of the same side are connected dorsally by longitudinal trunks. Malpighian tubules six in number. Ovaries with five ovarioles. Heart with nine pairs of ostia. The principal families of this order are the Lepismatidæ, Nicoletidæ, Maindroniidæ, and Gastrotheidæ. With regard to the Gastrotheidæ, it may be remarked that Silvestri, 1912_a, has shown that these insects belong to the Lepismid group, and that the supposed springing organ described by Casey is the ovipositor, which is somewhat similar to that of *Atelura* and related genera. Cook, 1901 (Proc. Ent. Soc. Washington, IV, p. 53) considered it so different from other insects that "he thought it necessary in consequence, to admit at least a new sub-order, which he would call Gastrotheoidea," and Handlirsch, 1906, raised it to an order, although he thought this a matter of some doubt. Silvestri, however, has shown that the insect in question is one of the Lepismid group.

SUMMARY.

The principal points brought out in the preceding discussion may be briefly summarized as follows. Crustacea (*e. g., Bathynella, Anaspides, Ligia,* etc.) "Myriopoda" (*Scolopendrella, Scutigera,* etc.) and the lower insects (*e. g., Eosentomon, Anajapyx, Machilis*) form the three apices of a triangle, each apex of which is connected with the other two by mutual bonds of relationship. These three groups are related to the Trilobita (such as *Triarthrus,* etc.), and through the Trilobites they are rather distantly related to Limulus and the Arachnids, but the Arachnid line of development diverges markedly from that of the three groups mentioned above as shown in fig. 2. The ancestors of Arthropods in general, were doubtless related to Annelidan worms and to *Peripatus.*

The Apterygota have retained characters suggestive of both Crustacean and Myriopodan affinities, and some of the Apterygotan lines of development are nearer to the Crustacea than to the "Myriopoda" in certain respects, while others are clearly much nearer to the "Myriopoda." The Apterygota as a whole doubtless arose from ancestors occupying a position intermediate between the Crustacean and "Myriopodan" lines of descent, as shown in the diagram, fig. 2). The Apterygota are much more primitive than their nearest Pterygotan relatives (the Blattids, Plecoptera and Ephemerids) and have departed the least from the probable ancestral condition of the Hexapoda, despite Handlirsch's contention to the contrary.

There are three main lines of development (possibly only two) in the Apterygota. These consist of the insects grouping themselves about the Protura, Rhabdura, and Thysanura, and they are divided into three sections termed the Proturadelphia, Rhabduradelphia, and Thysanuradelphia. The first group constitutes the non-styli-bearing Apterygota (Astyligera), while the last two constitute the styli-bearing Apterygota (Eustyligera). These may be further divided into seven or more orders represented by the Dasyleptidæ (?), Machilidæ, Lepismatidæ, Campodeidæ, Japygidæ, Eosentomidæ, and Entomobryidæ (with the Sminthuridæ ?).

As a whole, the Eosentomid group is the most primitive. The Entomobryids, Sminthurids, etc., are rather closely related to the Protura, but represent more or less degenerate offshoots which

branched off at a comparatively early stage of development (see fig. 1).

The "Rhabduran" insects with their concealed mouthparts, vestigeal first abdominal legs, etc., appear to approach the Proturan forms on the one hand, and also lead up to the *Machilis*-like forms with well-developed cerci, styli, etc., on the other: so that they might be regarded as somewhat intermediate between the two groups, although their closest affinities are with the Thysanuran group (*i. e., Machilis, Lepisma,* etc.). Such forms as Anajapyx serve to connect the Campodeidæ with the Japygidæ.

The Thysanuran group (*Machilis, Lepisma, Nicoletia,* etc.) approaches quite closely to the lower Pterygotan forms, the Plecoptera, Blattidæ, and Ephemeridæ being as nearly related to them as any of the Pterygota.

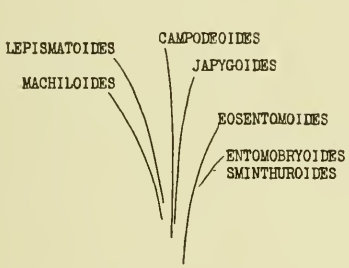

Fig. 1

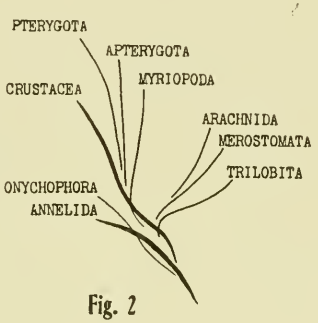

Fig. 2

The relationships of the principal Apterygotan groups are represented in fig. 1, while in fig. 2 the lines of descent of the more important groups related to the Insecta have been shown. It is impossible to represent the rather complicated interrelationships of the different groups in a figure drawn in one plane, since the various lines of descent approach one another from different angles, and it is practically impossible to represent this correctly without making such an intricate crossing of lines as to render the diagram almost unintelligible, and therefore useless. On this account, the discussion given above rather than the diagram, should be taken as setting forth the true relationships of the forms here described.

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